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Evaluation of Fishery Resources with Ecosystem Simulations and Quantitative Determination of their Response to Ocean Environmental Anomalies and Fishery

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ABSTRACT

Most marine fish stocks are near full exploitation. Some stocks have collapsed and some fluctuate considerably. There is an urgent need to 1) improve our capability to evaluate marine resources and their productivity, and 2) manage these resources to assure full utilization as well as preventing lasting harm to the marine ecosystem.

Large, holistic marine ecosystem simulations are replacing the earlier single-species and production models for resource evaluation and for the study of the dynamics of these resources. Because the pathways of the utilization of primary production in the sea are very variable in space and time and quantitatively ill known, the new holistic ecosystem simulations are "up the food chain" types, usually biomass based, and predation oriented. They utilize most of the available accumulated knowledge on the dynamic interactions in the marine ecosystem. These simulations are used for determination of equilibrium biomasses (carrying capacity) in different ocean regions. Some of the results obtained with these models are 1) the total finfish biomass varies from about 3 t/km^2 in low-latitudes (open ocean) to a maximum of 60 t/km^2 on highly-productive continental shelves in medium latitudes; 2) the North Sea finfish biomass is about 25 t/km^2; and 3) the Bering Sea has about 37 t/km^2, of which about 12 and 16 t/km^2, respectively, is exploitable. Sustainable annual yield in both cases is about 7.5 t/km^2. The important "production buffers" for finfish are benthos and zooplankton. The resources on continental shelves are dependent on production in offshore regions. The continental shelf areas are biological sinks (i.e. mortalities, including predation, are higher than growth of biomass).

Empirical data as well as ecosystem simulations show that individual species biomasses fluctuate considerably over the years. However, the total finfish biomass fluctuates but little with time, although pronounced, persistent, negative temperature anomalies cause some lowering of total biomass in high latitude regions. The average period of the fluctuations of individual species biomasses is 3 to 8 years (species dependent), and the magnitudes are about 70% of individual equilibrium biomasses. However, the highest biomass can be several times the lowest biomass. Rates of annual changes vary from about 8% of annual biomass (flatfishes) to about 45% (short-lived pelagic fish). Long-period fluctuations (decade to several decades) are superimposed on these shorter fluctuations. The fluctuations are mostly caused by environmental (e.g., temperature) anomalies, but can be modified by intensive fishery and by inter-species interactions (mainly predation).

TABLE OF CONTENTS

INTRODUCTION

The marine fish catch increased rapidly in the 1970's and leveled off in the beginning of the 1980's, indicating that marine resources might be close to full exploitation. Some pelagic resources collapsed in 1970's. However, some heavily fish stocks, such as groundfish in the North Sea, increased against conventional concepts of the behavior of fished stocks. Most fish stocks fluctuate in abundance with time even without fishery.

As the food resources of the world are limited, there is a requirement to utilize the marine resources fully, applying wise management measures. This requires accurate knowledge of the resources and their dynamics. Conventional marine resource evaluation methods which are based on single-species concepts, have serious limitations. For example, a fishery that targets on one species affects nontarget species via interspecies interactions (mainly predation). Needed, therefore, is a holistic ecosystem approach to resource evaluation, management, and study of the dynamics of the marine resources and their response to environmental changes. A review of the holistic ecosystem approach for resource evaluation is given in this paper, together with examples of some results.

METHODS USED IN THE EVALUATION OF ABUNDANCE AND DYNAMICS OF MARINE RESOURCES

All empirical sampling methods for survey of marine resources are very expensive (re. expensive ship time) and have shortcomings due to dispersed nature of the resources and their inaccessibility. First, the catchability of different species varies in space and time and with the gear used, and it is nearly impossible to determine the catchability factor with desirable accuracy. Second, the distribution of the resources is patchy and this patchy distribution varies rapidly with time. Accurate resource surveys also require synopticity and intensive sampling. Despite these difficulties, we must continue with the resource surveys and should attempt to compliment them with other means which become available.
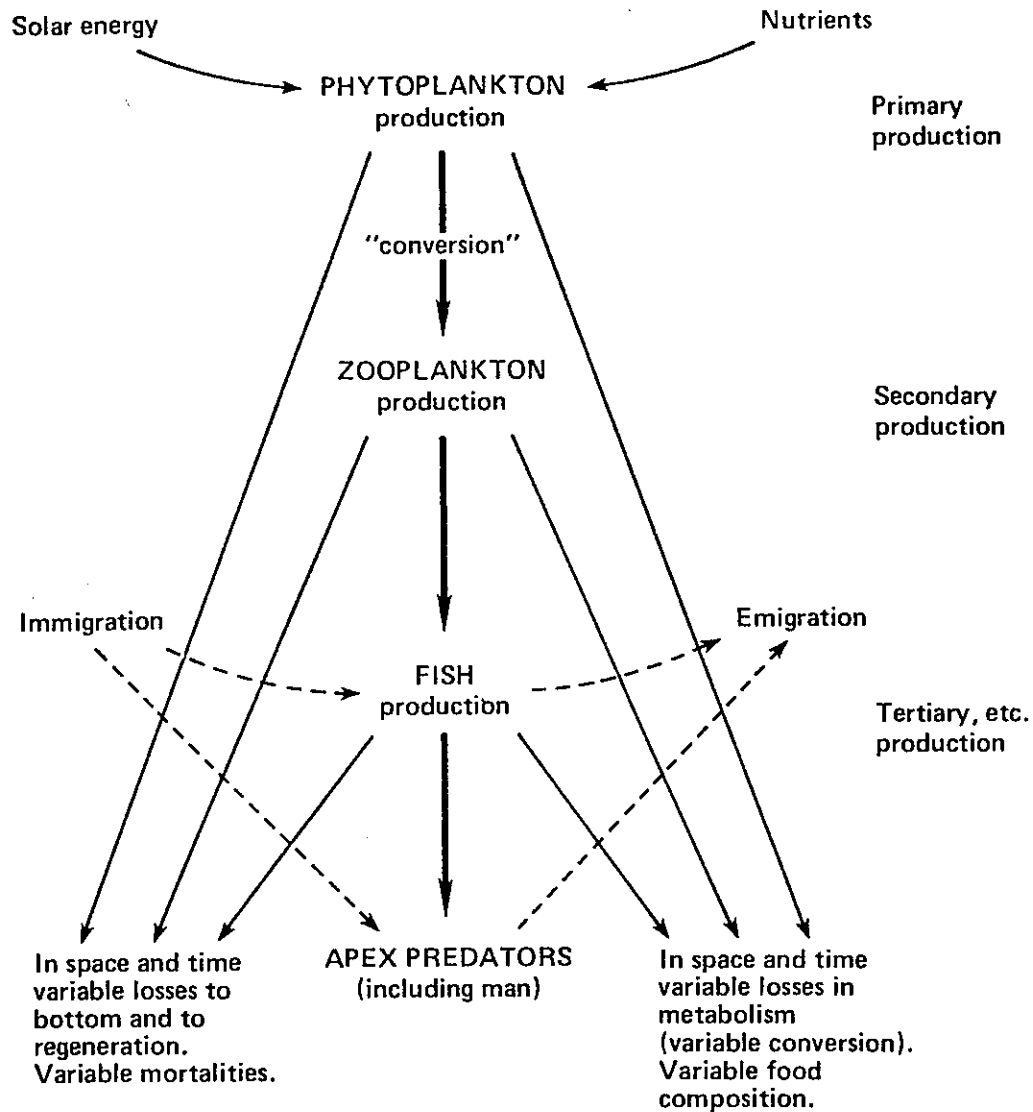
The acoustic survey methods are relatively rapid, but suffer many shortcomings: they require quasi-simultaneous survey with several ships in order to achieve good coverage and to eliminate the effects of migration. Furthermore, high-speed sampling is necessary to determine the species and its size which is being recorded by the acoustic gear. There are also difficulties with calibration of an acoustic signal, which varies from species to species and even with the cross-section aspect. Truly demersal species cannot be surveyed by acoustic methods. Nevertheless acoustic methods are of great utility in modern resource surveys.

Single-species population dynamics methods for resource evaluation and other methods closely related to them, such as cohort analysis, also have serious shortcomings. These methods use data obtained from commercial catches and their age compositions. First, these methods can be applied only as approximations on stocks which are under considerable exploitation and where sampling is

sufficient, such as in the North Sea. Each species is considered separately in these approaches without species interactions, such as predation. The natural mortality is not accurately known and is often applied as non-age specific. Furthermore, the spawning stock-recruitment relations are highly variable in most species. Some attempts have been made recently to develop multispecies virtual population analysis (legion analyses) by including estimations of predation.

Since the early 1920's various methods of computing marine production based on basic organic production have been used, assuming some "trophic levels" and transfer coefficients of organic matter (or energy) between these levels. Principles of these "production models" are given in Figure 1. Although a great number of estimates of marine production have been made using these principles, the reliability of these results is questioned. The main shortcomings of this approach are 1) the basic organic production is variable in space and time and not known with desired accuracy, 2) the utilization of this production by other ecological groups is also variable in space and time and ill-known, 3) trophic levels cannot be explicitly defined in the marine ecosystem as the composition of food varies with age (size) of the species, and also in space and time for the same species. Attempts have been made to overcome the last difficulty by prescribing food composition for various ecological groups and using "energy transfer coefficient" to compute the utilization of available food resources. These attempts have not been any more successful than the original production model.

As overly simplified approaches cannot be expected to yield realistic results in marine resource evaluation, it is necessary to embark on holistic marine ecosystem evaluation using all pertinent available information on the processes in it.

Figure 1.--Principles of conventional "production models" for estimation of mean standing stocks and production in the oceans.

PRINCIPLES AND FORMULATIONS OF BIOMASS BASED HOLISTIC ECOSYSTEM SIMULATIONS.

The principles of a trophodynamic ecosystem evaluation are given in Figure 2. The basic computation of this evaluation is to determine how much of the biomass of different species (or ecological groups) is consumed (and dies) per unit time in the given ecosystem. Given biomass growth rates the levels of the biomasses which can produce the consumed amounts can be computed with an iterative procedure. Mathematically it means to find a unique solution to a series of biomass balance equations. The basic formulas and computation procedures are given in the appendix. The simulation models have been described in detail by Laevastu and Larkins (1981).
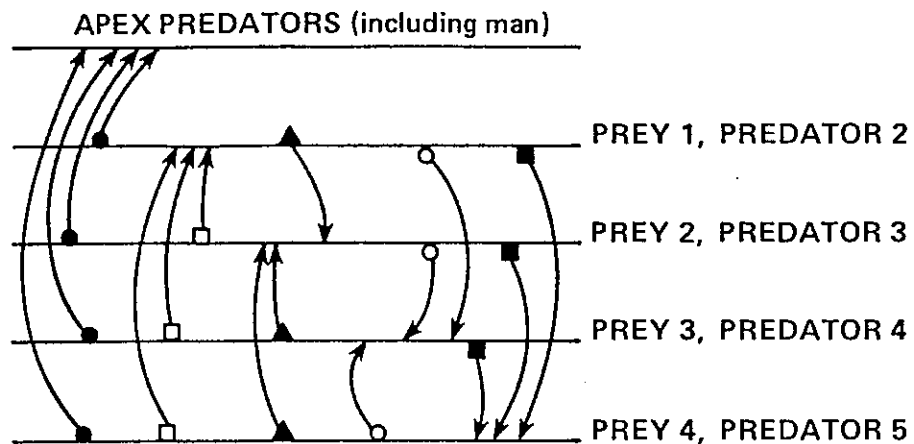
The essential processes in marine ecosystem are schematically shown in Figure 3. Figure 4 gives the examples of geographical setting of ecosystem simulations. It should be noted that one uses homogenous "boxes", and the other the grid method for subdividing the area. The latter model (DYNUMES) is a more flexible and accurate model, allowing the computations of migrations and other spatial effects.

The ecosystem simulation can be characterized as: numerical quantitative reproduction of a system by structural parts of it, using deterministic formulations justified by empirical data, i.e., a Pythagorean dictum.

Some of the requirements of holistic ecosystem simulations would help to understand their utility:

—The simulations must include all components of the biota, all essential environmental factors, and all essential processes within the ecosystem.

—Mathematical formulas in the simulation must serve for quantitative reproduction of known processes. Explicit approaches, free from mathematical artifacts, must be preferred.

APEX PREDATORS (including man)

PREY 1, PREDATOR 2

PREY 2, PREDATOR 3

PREY 3, PREDATOR 4

PREY 4, PREDATOR 5

Principles: Determine who eats what and how much. Then determine how
                much of the prey must be there to produce the eaten amounts.
                (Food requirements and growth rates known, biomass can
                be determined.)

Advantages: Minimum values of the production and standing stocks of all
                prey can be computed.

                Amounts of noncommercial (and nonsampled) species
                can be estimated.

                Changes in one prey biomass are related to changes in other
                prey biomass via predation.

Figure 2.--Principles of trophodynamic ecosystem computations, based on
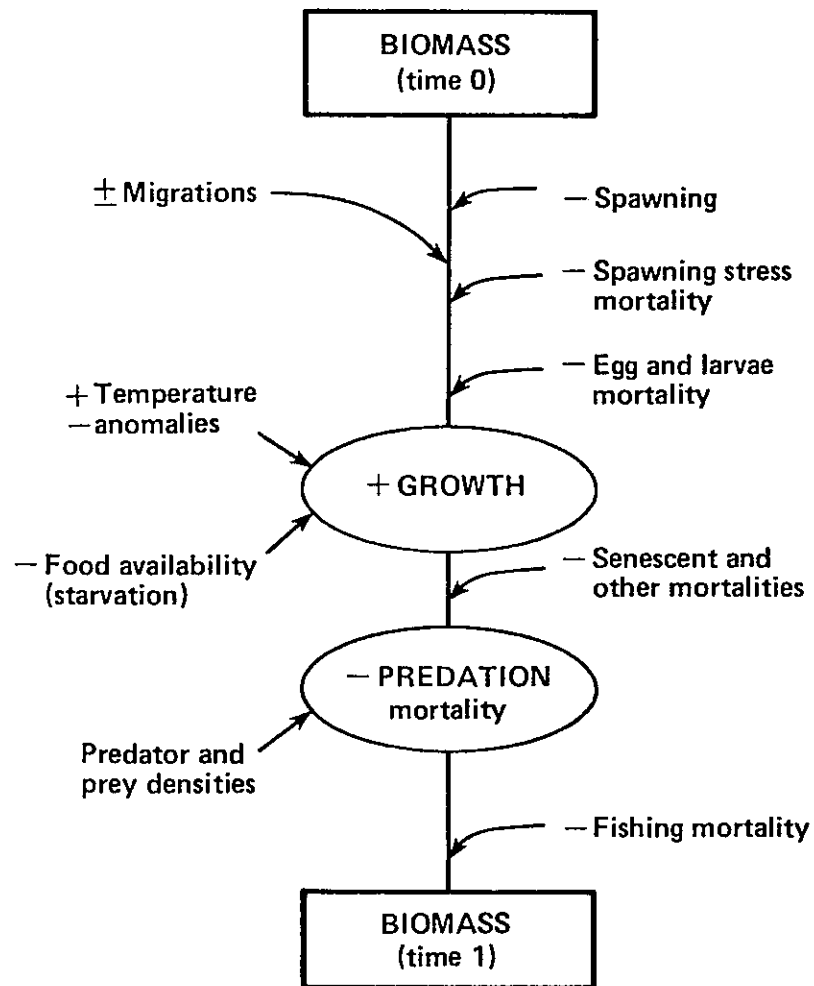   food requirements.

Figure 3.--Scheme of principal processes and interactions in a species in the marine ecosystem.
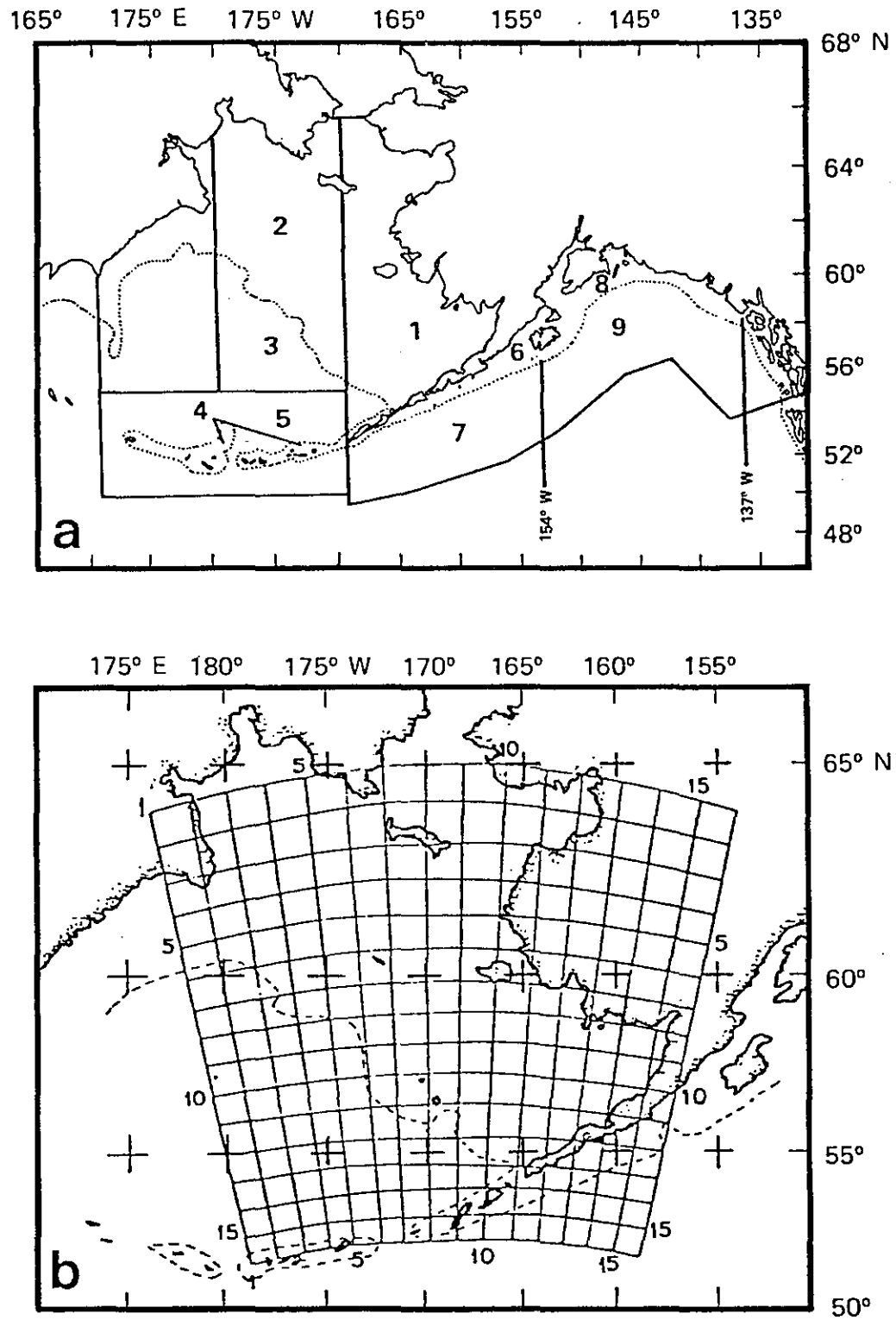
Figure 4.--Computation areas used in PROBUB model for Bering Sea and Gulf
of Alaska and computational grid for DYNUMES model for the eastern Bering
Sea.

—The formulation must not be conditionally stable, except for one unique solution (i.e., for determination of equilibrium biomasses).

—Simulations must be tailored to available data, to void uncertain guesses.

—The simulations require the use of the largest computers.

The comparison of traditional number-based models and biomass-based models is given in Table 1.

Verification of large ecosystem simulations is done by its components. This involves testing whether they reproduce empirically known results and are otherwise correct according to our recent knowledge. Validation of the results are carried out by comparing them to various independent survey results. It is also possible to evaluate the probable errors of simulations by assigning plausible minimum and maximum values to uncertain input parameters as well as to quantitative formulations. A schematic presentation of the error and "sensitivity" tracing is given in Figure 5. Table 2 gives some estimated plausible maximum error limits of equilibrium biomasses in the PROBUB model; the error limits have been derived through the use of the abovementioned probable error evaluation procedure.

EQUILIBRIUM BIOMASSES (CARRYING CAPACITIES) IN VARIOUS OCEAN REGIONS

Ecosystem simulation model PROBUB has been used for the evaluation of equilibrium biomasses (standing stocks), their consumption and turnover rates from the Bering Strait to the Mexican border. Results of detailed computations in the Kodiak area in the northern Gulf of Alaska (Figure 6) are presented in this paper. The biomasses of different species and ecological groups in coastal, continental slope, and offshore subregions are given in Table 3. Table 4 gives a corresponding summary on the plankton parameters, the production of which sustains

Table 1.--Comparison of some properties of number and biomass based multispecies models.

Number-based models	Biomass-based models
1. Need to divide all species into year classes.	1. No need to divide into year class.
2. Need to convert often from numbers to weight.	2. No need to convert to numbers.
3. Errors in "number reduction" over-magnified.	3. Errors in predation "buffered" to a large degree.
4. Effects of growth rate variations difficult to handle.	4. Growth rate variations easy to handle in numerical schemes.
5. Recruitment mostly discontinuous and sensitive to predation.	5. Recruitment "continuous" and easy to handle.
6. Food composition determined mainly by size components.	6. Food composition variable and easy to handle.
7. Effects of environment and starvation difficult to handle.	7. Environmental effects easy to incorporate.
	8. "Back down the food chain" computations possible.
	9. Migrations easy to handle
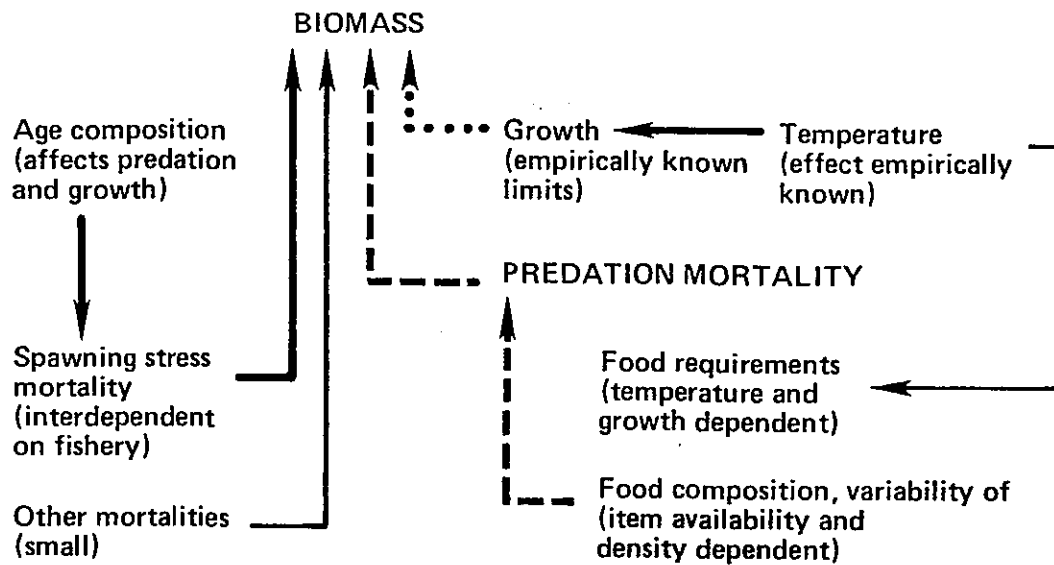
Figure 5.--"Scheme of influence" on plausible error in the determination of biomass of any species in the ecosystem simulation. ——minor effects; ▬▬moderate effects, but error limits controlled by empirical data; ...major effects, but errors limited with reliable empirical data; ---major effects, variable in space and time.

Figure 6.--Computation subareas in PROBUB model for Kodiak region in northern Gulf of Alaska (1, 11, 12 - coastal areas; 2, 5, 8, 13 - continental shelf areas; 3, 6, 9, 14 - slope areas; and 4, 7, 10, 15 - oceanic areas).

Table 2.--Estimated plausible maximum error limits of equilibrium biomasses
in PROBUB (in percentage of plausible mean value)

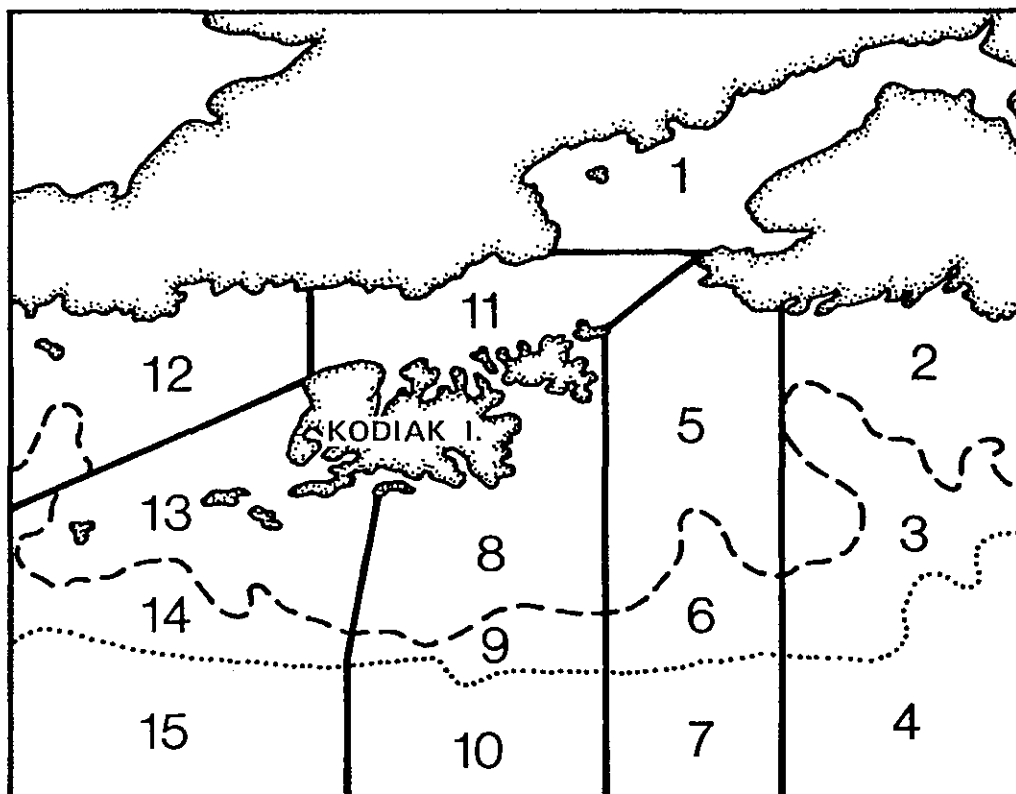| Ecological group	Maximum error limits (%)	Remarks on largest plausible source of errors
Flatfishes	18	Seasonal changes in food uptake and composition due to seasonal depth migrations
Pollock	20	Spatial change of growth rate and offshore distribution of biomass during some seasons
Herring	25	Seasonal and spatial changes in contribution of herring and
Rockfishes	30	rockfishes to food of other species; seasonal migrations
Cod, sablefish	20	Growth rates of juveniles, seasonal migrations
Other noncommercial demersal	25	Growth rates; size-age distribution; occurrence in diet of other
Other noncommercial pelagic	30	species; age of maturity and senescent mortalities
Crabs, shrimps	25	Growth rates, distribution (spec. of juveniles)

Table 3.--Mean biomasses of some species and ecological groups in coastal, continental slope, and oceanic subregions in Kodiak area, as computed with PROBUB model.

Species and/or ecological group	Coastal subregions	Slope subregions	Oceanic subregions
	----------------tonnes/km^2-------------------		
Herring	7.32	3.03	1.71
Other pelagic fish	12.47	12.62	7.32
Squids	2.54	2.31	1.52
Salmon	0.41	0.34	0.37
Rockfishes	2.45	1.57	0.44
Gadids	6.74	4.52	1.32
Flatfishes	3.10	1.87	0.42
Other demersal fish	3.84	3.30	0.65
Crustaceans (commercial)	7.15	3.62	1.34
Benthos ("fish food" benthos)	36.85	19.42	3.39

Table 4.--Estimated plankton productions, standing stocks, and their annual
consumption in coastal, continental slope, and oceanic subregions
in Kodiak area using PROBUB model

Subject	Coastal subregions	Slope subregions	Oceanic subregions
	---------------tonnes k/m^2---------------		
Annual mean phytoplankton production and mean	1500	1350	1000
standing crop	200	180	135
Annual mean zooplankton production and mean	225	180	200
standing stock	45	36	40
Annual phytoplankton consumption by nekton	20	14	6
Annual phytoplankton consumption by zooplankton	241	194	220
Annual zooplankton consumption by nekton	129	123	58
Annual consumption of detritus by benthos	133	70	12

the fish production.   Benthos on the continental shelf is important in sustaining the demersal and semidemersal fish biomasses and recycling the detritus which constantly sedimentizes down to the bottom.

Presented in Table 3 are the total biomasses (i.e., including prefishery juveniles) for selected species and ecological groups.   These estimates are somewhat higher than many produced from alternative estimation procedures in the past.   A partial reason for this is that our models do not use strictly defined "trophic levels", and as fish eat fish (i.e., larger fish feed on smaller fish); consequently, the fish biomasses constitute also a food source to each other, and effect therewith "recycling" and widened food base.

The annual production of fish biomasses, which are proportional to turnover rates, are summarized in Table 5, together with data on average fraction of biomass (standing stock) consumed monthly.   From this table we can conclude that benthos biomass reproduces its mean standing stock 1.2 to 1.7 times annually. The pelagic fishes reproduce their biomass annually and the flatfishes reproduce 0.4 to 0.7 times their biomass annually.

Using the results from the ecosystem application in various regions in the northeast Pacific and other similar approaches elsewhere (e.g., Andersen and Ursin 1977 in the North Sea), and comparing the available quantitative knowledge of factors affecting productivity, a generalization of the estimation of marine fisheries resources in terms of biomass per unit area has been made in Table 6. We have estimated the limits of exploitable biomasses as well as possible fishery yields.   The actual yields depend on the demand for species and changes in the ecosystem which occur with time.   Examples of the utilization of finfish biomass in the North Sea and in the Bering Sea are given in Table 6.

Table 5.--Normal ranges of turnover rates of biomasses in marine ecosystem.

Species-ecological group	Turnover rates
Flatfishes	.35 to .70
Semipelagic fishes (gadids)	.65 to .80
Pelagic fishes	1.0 to 1.1
Squids	1.7 to 2.0
Shrimps	.70 to .95
Crabs	.50 to .65
Benthos	1.2 to 1.7

Table 6.--Finfish biomasses and their utilization in the North Sea and in the
   Bering Sea).

Biomass utilization	North Sea	Bering Sea
	----------tonnes k/m^2-------------	
Total finfish biomass	25	37
Present catch	6.7	1.9
Consumption by mammals	0.1	3.1
Consumption by birds	0.3	1.1

There are some biomasses of considerable magnitudes in the open oceans which are not accessible to man--those are bathypelagic fish (such as myctophids) and squids. A computation of squid biomass in the North Pacific (Table 7) indicates the magnitudes of these resources.

Table 8 shows that over the continental shelves there are many times higher standing stock of finfish than in the open ocean. It does not follow that the basic organic production is equally much higher over the continental shelf. However, somewhat higher basic organic production occurs over continental shelves in mid-latitudes, mainly due to provision of nutrients to surface layers by wintertime mixing and turnover of water, which brings up the nutrients from bottom layers where they have accumulated during summertime decomposition of organic matter on the bottom. Furthermore, there is an intensive "recycling" of organic matter by benthos, which constitutes another food source for finfish biomass.

The high biomasses over continental shelf are also a manifestation that these are sink areas of finfish biomass (i.e., the mortalities from all causes exceed the growth of biomasses, especially of pelagic and semipelagic species). The reason for this is that prefishery juveniles of many species spend the juvenile years in offshore regions and return to coastal areas for spawning and for their adult life.

FLUCTUATIONS IN ABUNDANCE OF FISH STOCKS

Availability and catches of different species fluctuate considerably in space and time. Research results show that the stocks of some species decrease and others increase with time, whereas total fish biomass in a given region seems to remain relatively constant.

Table 7.--Estimation of consumption of squids by sperm whale in the North Pacific.

175,000 [1] harvestable sperm whales in the North Pacific

30 tonnes mean weight

= 5.25 million tonnes biomass

5% [2] BWD (body weight daily), food requirement

= 18.25 times body weight annually

= 95.81 million tonnes total food consumption

Food composition:

85% [3] squids

15% fish

Annual consumption by sperm whales in North Pacific:

= 81.4 million tonnes squids

14.4 million tonnes fish

Assuming $F_{max} \approx 20\%$ [4], the minimum biomass of squids in the North Pacific

$\approx$ 400 million tonnes.

1/ This is an "absolute minimum" estimate (Int. Whaling Comm. Spec. Issue 2, 1980).
The total number of sperm whales in the North Pacific is estimated for 1977 as:
females 411,000 to 525,000; males 376,000 to 474,000.

2/ The food consumption of whales is estimated in literature to 4 to 6% BWD. The
minimum estimate is 2.5% BWD.

3/ Some estimates give up to 95% squids.

4/ This "fishing coefficient" of squids by sperm whale is probably too high; it
corresponds roughly to F of pelagic fish.

Table 8.--Estimated biomasses of fish, exploitable biomasses, and estimated annual yields in different ocean regimes (from Laevastu and Hayes 1981).

Type of area characteristics	Total finfish biomass	Exploitable biomass	Sustainable annual yield (intensive fishery)
	------------tonnes k/m^2------------------		
(1) Open continental shelves with upwelling type circulation			
Tropics	25 to 45	8 to 15	3 to 7
Medium latitudes 1/	40 to 60	12 to 20	4.5 to 8
Higher latitudes	30 to 40	11 to 17	3.5 to 5.5
(2) Open continental shelves, no upwelling type circulation			
Tropics	15 to 30	4 to 10	1.8 to 4
Medium latitudes	25 to 45	8.5 to 12	4 to 6
Higher latitudes	20 to 35	8 to 14	2 to 4
(3) Wide marginal seas (e.g., North Sea)	25 to 45	9 to 18	6 to 7.5
(4) Semi-closed seas, Mediterranean type circulation	12 to 25	4 to 8	1.2 to 2.0
(5) Semi-closed seas, Baltic type circulation	18 to 28	5.5 to 9.5	2.2 to 3.5
(6) Open ocean			
Low latitudes	3 to 6	0.5 to 1.2	(<0.3) 2/
High latitudes	5 to 12	1.5 to 3	(<0.6) 2/

In items 1 to 5 above the biomass and yield estimates refer to areas shallower than 500 m.

1/ Assuming no great quantities of marine mammals present.

2/ These yields cannot be obtained due to dispersed nature of the resources.

Examples of short-term variations of catches of two species are given in Figures 7 and 8, which indicate irregular fluctuations with periods of 4 to 7 years. Superimposed on these shorter fluctuations are long-term trends. The higher the biomass, the higher is the magnitude of fluctuations (Figure 8).

The major factors affecting the fluctuations of fish stocks are summarized in Table 9. An example of the computed fluctuations, using PROBUB model, is shown in Figure 9 depicting the fluctuations of Pacific cod biomass in Bristol Bay (in Bering Sea). Also shown on this figure is the consumption (predation) of cod. The predation on cod larvae and juveniles is dependent on their density as well as on the density of predators present. The density dependent predation acts as a "stabilizing mechanism", i.e., limits the magnitudes of fluctuations.

Table 9.--Major factors causing fluctuations in marine fish ecosystem.

| Factors	Main effects
External factors	
Temperature anomalies	Changing metabolic rate (affecting growth and food uptake)
Fishing	Changing abundance of older biomass, thus affecting predation, cannibalism, and recruitment
Internal factors	
Predation (including cannibalism)	Affecting recruitment; main mechanism in interspecies interaction in predator-prey system
Competition	Interspecies interaction in predator-prey system; starvation (affecting growth)
Migrations	Changing predator-prey system by changing predator-prey overlap (local density)
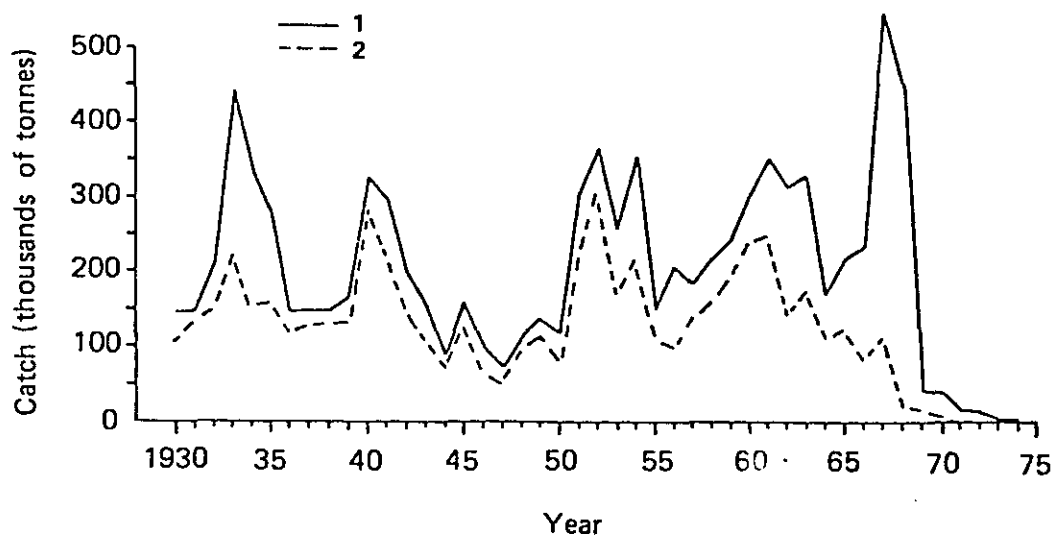
Figure 7.--Catch of young and adolescent Norwegian herring in 1930-1974 (from

Dragesund et al, 1980); 1- total catch; 2 - small herring).
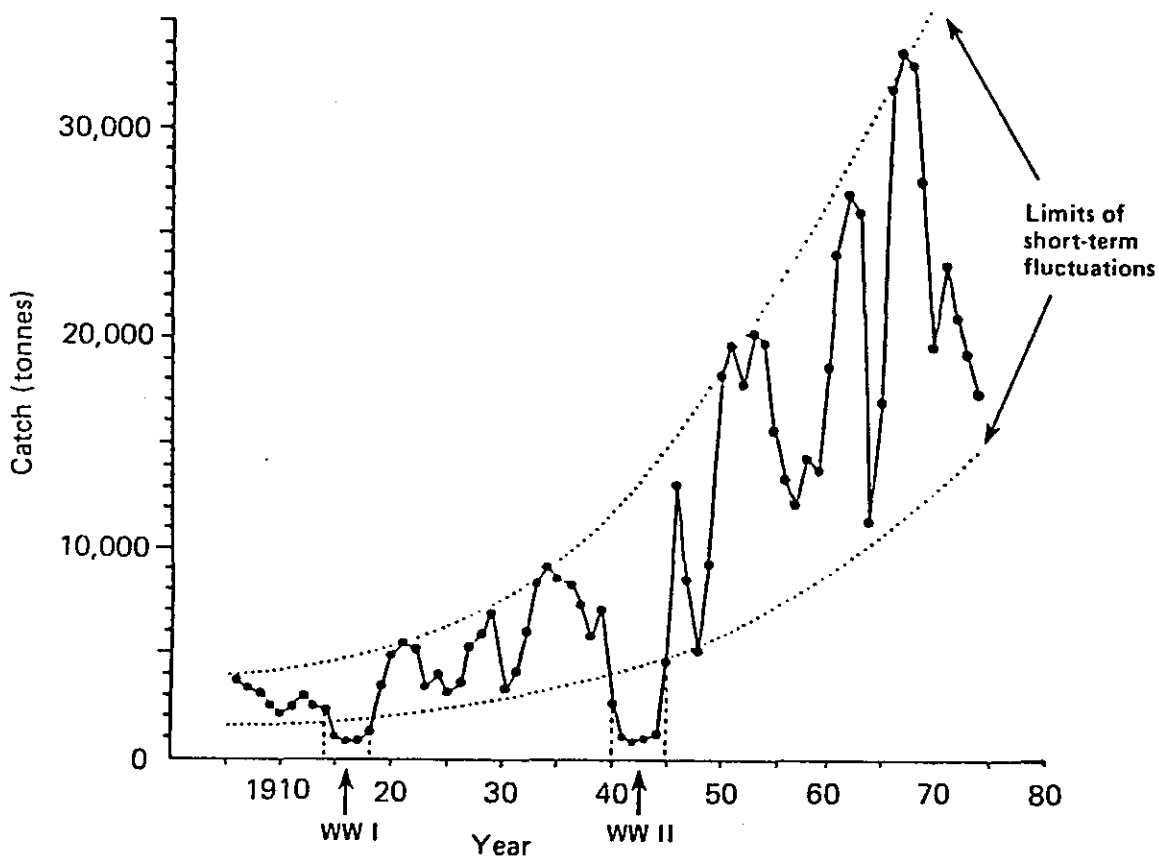

Figure 8.--Total international landings of North Sea sole (after De Veen,
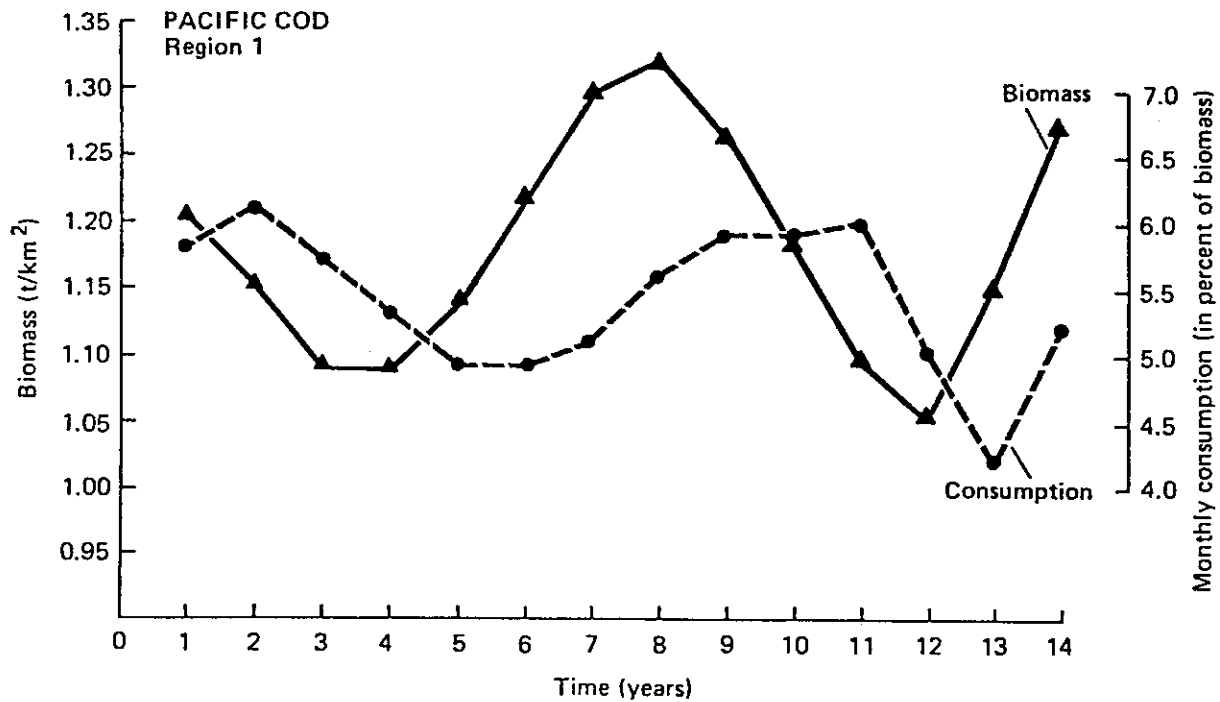
1978).

Figure 9.--Fluctuations of Pacific cod biomass in Region 1 in Bering Sea (see Figure 4) and the consumption of cod (in % of biomass) by the ecosystem.
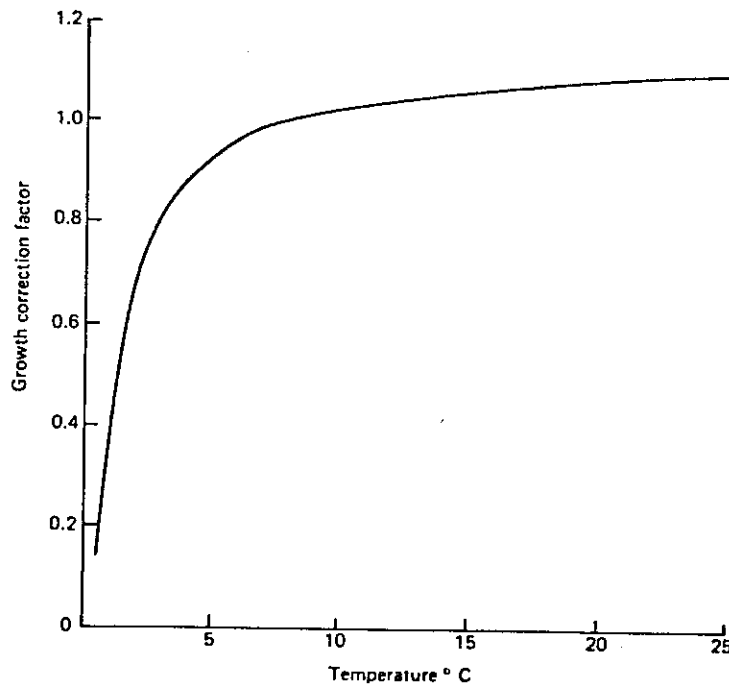

Figure 10.--Effect of temperature on growth rate, with an acclimatization temperature of 8°C (formula see Appendix).

EFFECTS OF ENVIRONMENTAL ANOMALIES ON THE FLUCTUATIONS OF FISH BIOMASSES

The effects of temperature anomalies on the fish biomasses can be studied quantitatively with ecosystem simulation models. One of the well-known and main effects of temperature on the fish is the effect on growth rates (Figure 10). The studies with the PROBUB model indicates that the effects of temperature anomalies vary from region to region, as they depend on the acclimatization temperature of the stock. The largest effects are observed at high latitudes where the fish are found close to their natural environmental boundaries. There is also a difference between the effects of negative anomalies and positive anomalies and whether the anomalies occur during summer or during winter. This variation of the temperature effect explains why the empirical studies, which attempt to search simple correlation between temperature and fish abundance, have often failed.

Annual anomalies, lasting more than one year, cause changes in biomass which can last for many years after the anomaly. Figure 11 shows how the pollock biomass is affected by anomalies in year 1 to 3 of the following magnitude (+0.7^{o}C first year, +1.4^{o}C second year, and +0.7^{o}C third year; in analog -0.7-1.4; -0.7).

The temperature anomaly effects can be reversed on predominantly forage (prey) species such as capelin (Figure 12), and can be delayed in respect to anomalous years. These shifts and delays are caused by the changes in predation (i.e., increase or decrease of predator biomasses). The effects of anomalies on demersal fish are usually short-lived (Figure 13).

The temperature anomalies affect also the fluctuations of biomasses, both in respect to magnitudes and periods (Figure 14). Again, these effects vary from species to species and region to region.
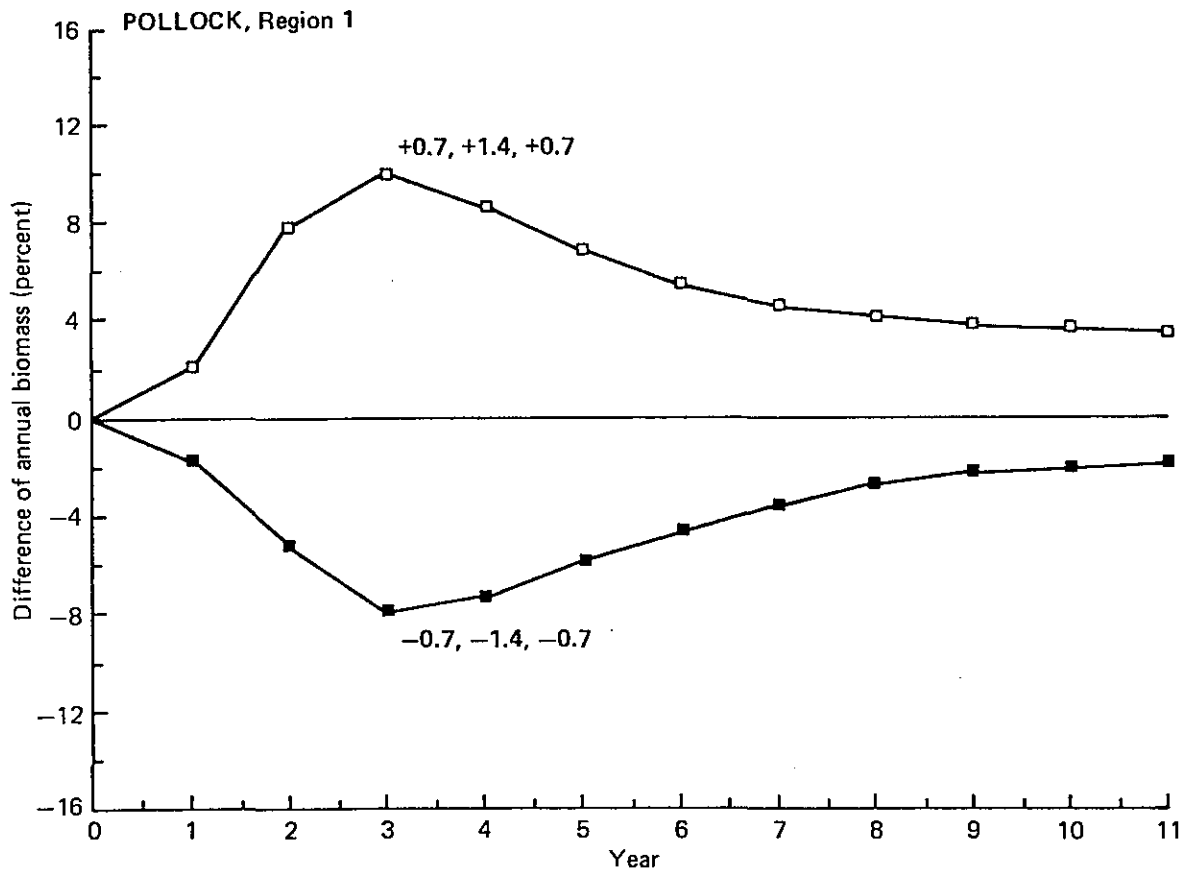
Figure 11.--Annual differences of biomass from "normal" biomass of walleye
pollock in Region 1 in Bering Sea (see Figure 4), caused by 3-year
temperature anomalies (±0.7; 1.4; 0.7° in first, second, and third year,
respectively).
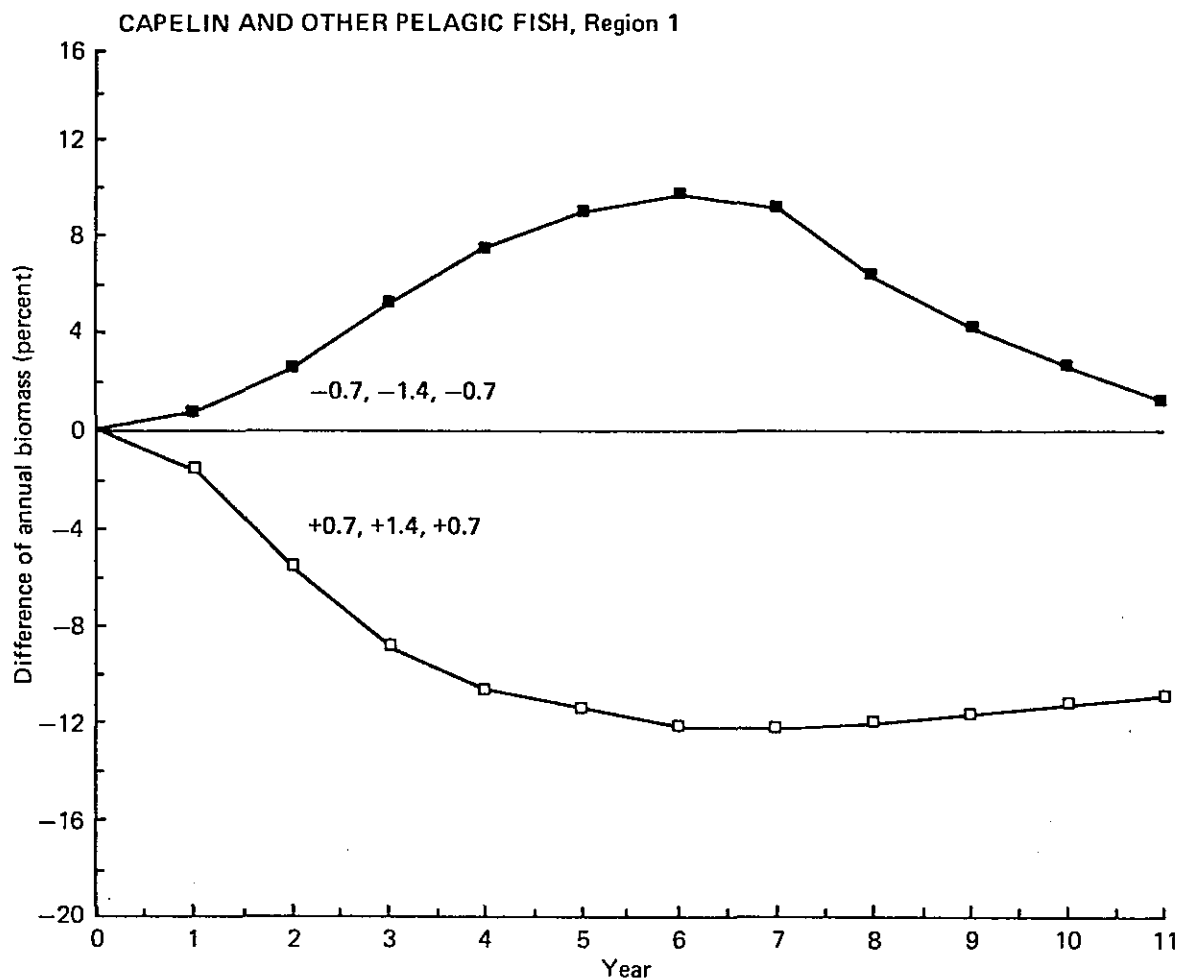
CAPELIN AND OTHER PELAGIC FISH, Region 1

Figure 12.--Annual differences of biomass from "normal" biomass of capelin and other pelagic fish in Region 1 in Bering Sea (see Figure 4), caused by 3-year temperature anomalies (± 0.7; 1.4; 0.7° in first, second, and third year, respectively).

Figure 13.--Annual differences of biomass from "normal" biomass of yellowfin

sole in Region 1 in Bering Sea (see Figure 4), caused by 3-year temperature

anomalies ($\pm$0.7; 1.4; 0.7° in first, second, and third year, respectively).
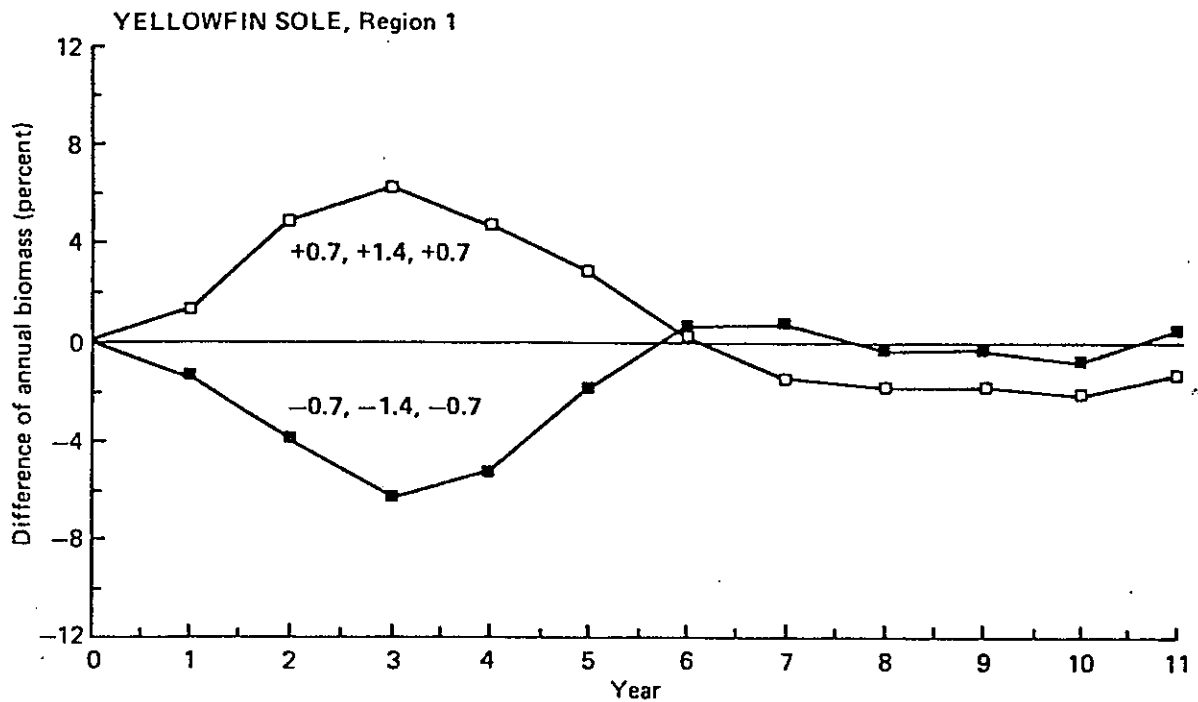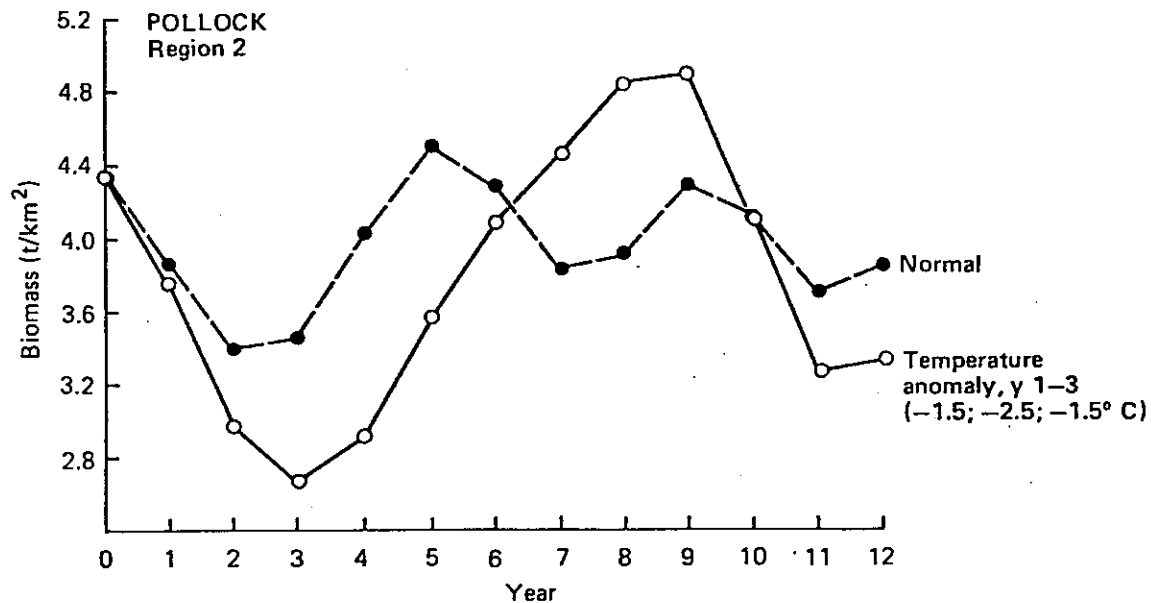

Figure 14.--Fluctuation of pollock biomass in Region 2 in the northeast Bering

Sea (see Figure 4) in "normal" condition and the same fluctuations with

temperature anomalies in years 1, 2, and 3 (-1.5; -2.5; -1.5°C, respectively).

EFFECTS OF FISHERY ON FISH STOCKS

Modest fishing affects fish stocks (abundance) little because the "density dependent predation" and inverse relations between spawning stress mortality (senescent mortality) and fishing mortality are compensatory (Figure 15). In some cases the fishing effects can be "overcompensated" by the rejuvenation effects (increased growth of young biomass), so that a modestly fished population increases above virgin population (Figure 16).

Heavy fishery, however, lowers the biomass of the target species (Figure 17, doubling of pollock catch in year 1) and lowers the magnitude of fluctuations. The effects of fishery can have opposite effects on the prey species as compared to target species (Figure 18).

Fish stocks fluctuate considerably in abundance, whereby the biomass of one species declines, another species biomass inclines. The total biomass of all finfish tends to remain relatively constant. A summary of the fluctuations of fish biomasses, as determined with PROBUB model is given in Table 10. The periods of fluctuations vary from 4 to 7 years. The magnitudes of fluctuations of fish biomasses vary from 35% to 80% of the mean equilibrium biomass, and can be as high as 120% in benthos (epifauna and infauna).

The total biomass of fish in a given region fluctuates less than 10% of its mean equilibrium biomass (Figure 19). Obviously, temperature anomalies and heavy fishery on abundant species affect the total biomass and its fluctuations somewhat. (In Figure 19 the predominant species in Region 1 - Bristol Bay - is pollock, and the temperature anomaly was -1.5°, -2.5°, $-1.5^{\circ}C$ in years 1 to 3)

Figure 15.--Changes of biomass without fishery (F=0) and with two different constant yields (F $\approx$ 0.1 and 0.2), and with fishing-spawning stress morality interaction (0.018 B_t (1 - $\frac{f}{ck}$)) (Laevastu and Marasco, 1982b).
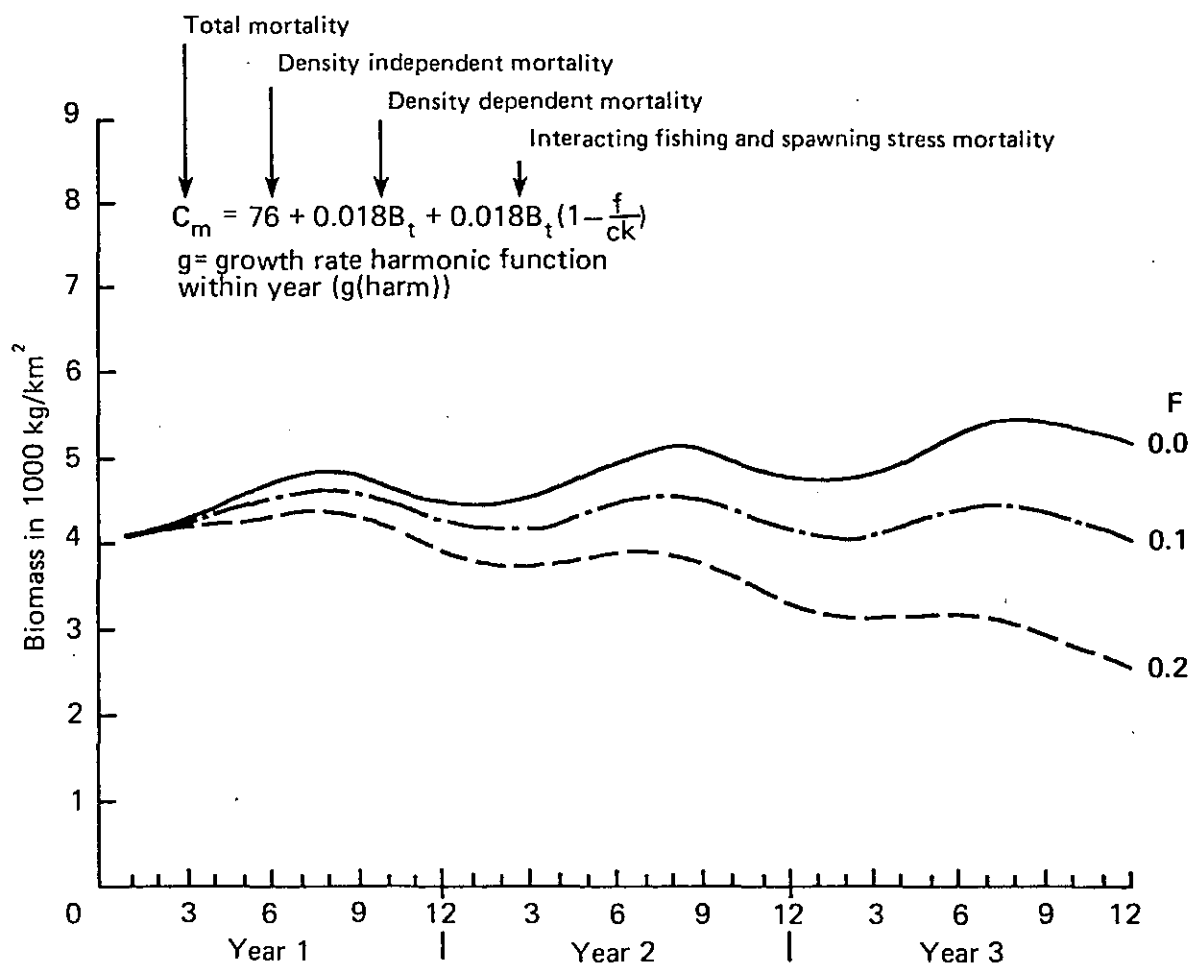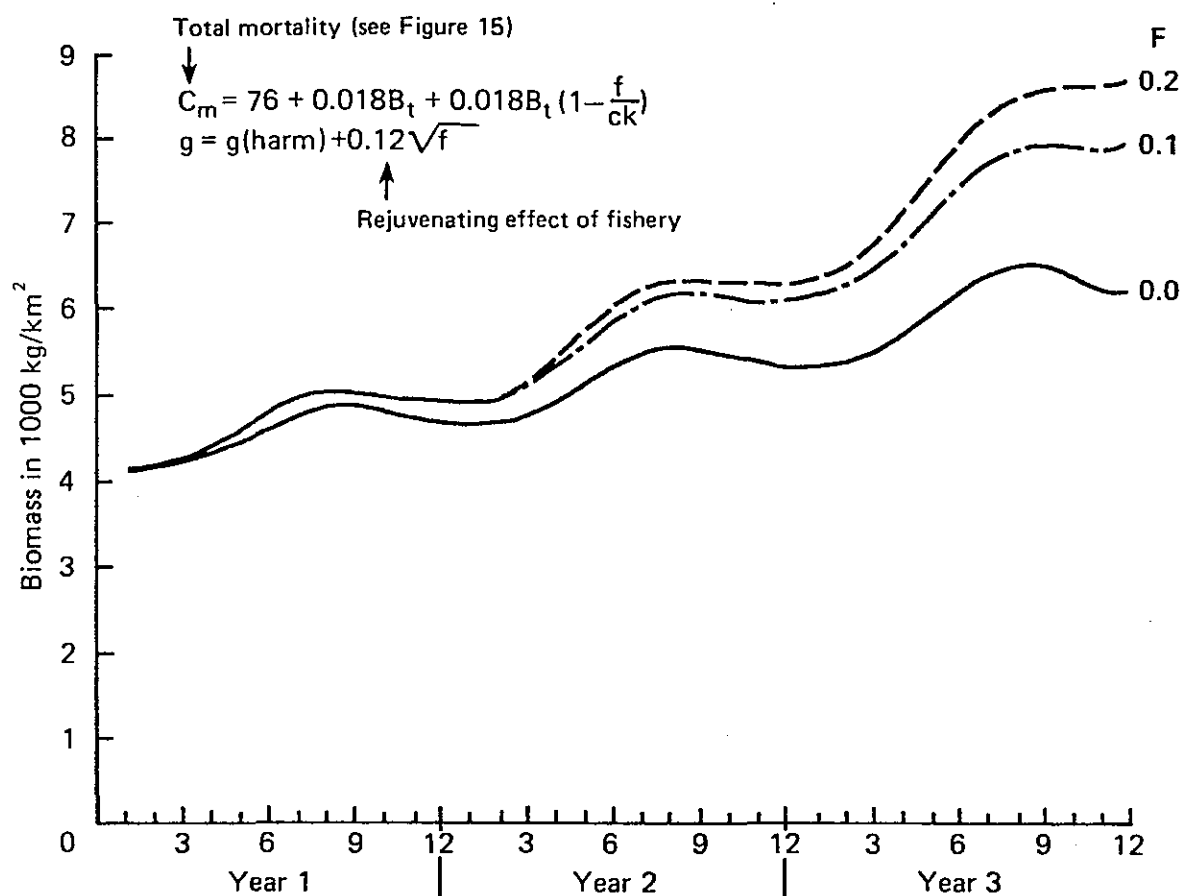
Figure 16.--Change of biomass without fishery and with two different constant yields, and with fishing-spawning stress mortality interaction and with rejuvenation effects on growth rate $(0.12\sqrt{f})$ (Laevastu and Marasco, 1982b).
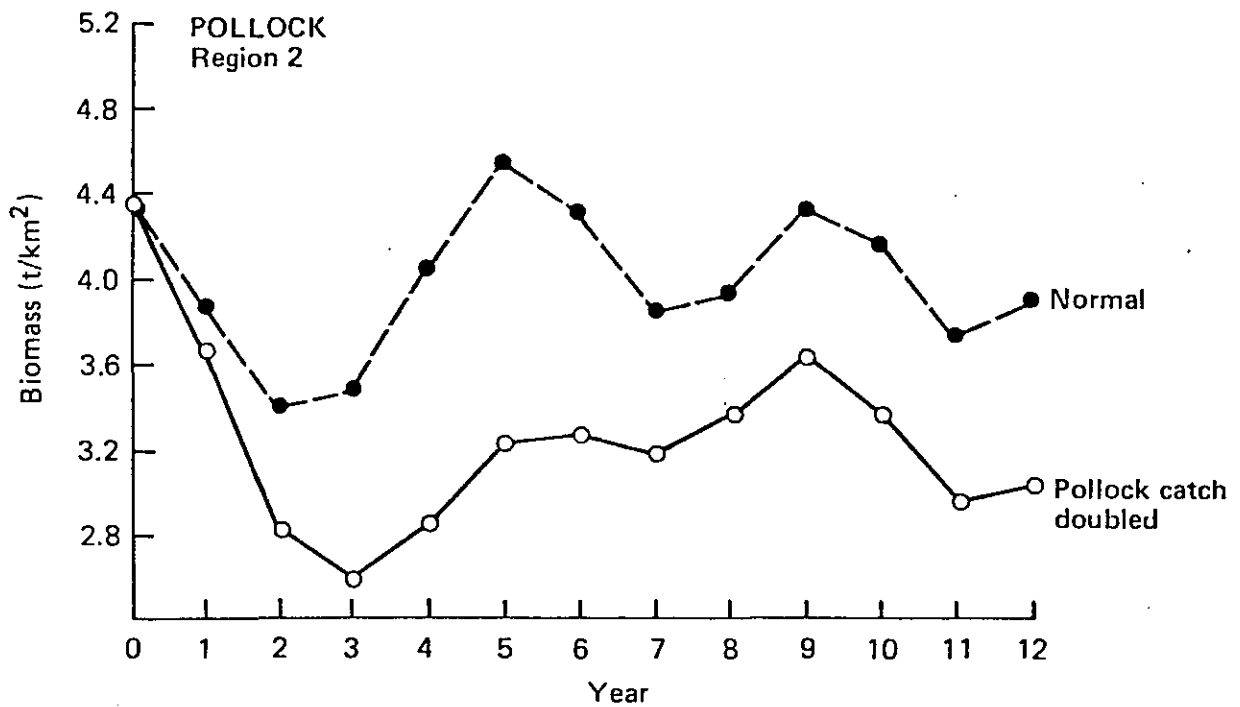
Figure 17. Fluctuations of pollock in Region 2 in the northeast Bering Sea (see Figure 4) with present catch ("normal") and with pollock fishery doubled.
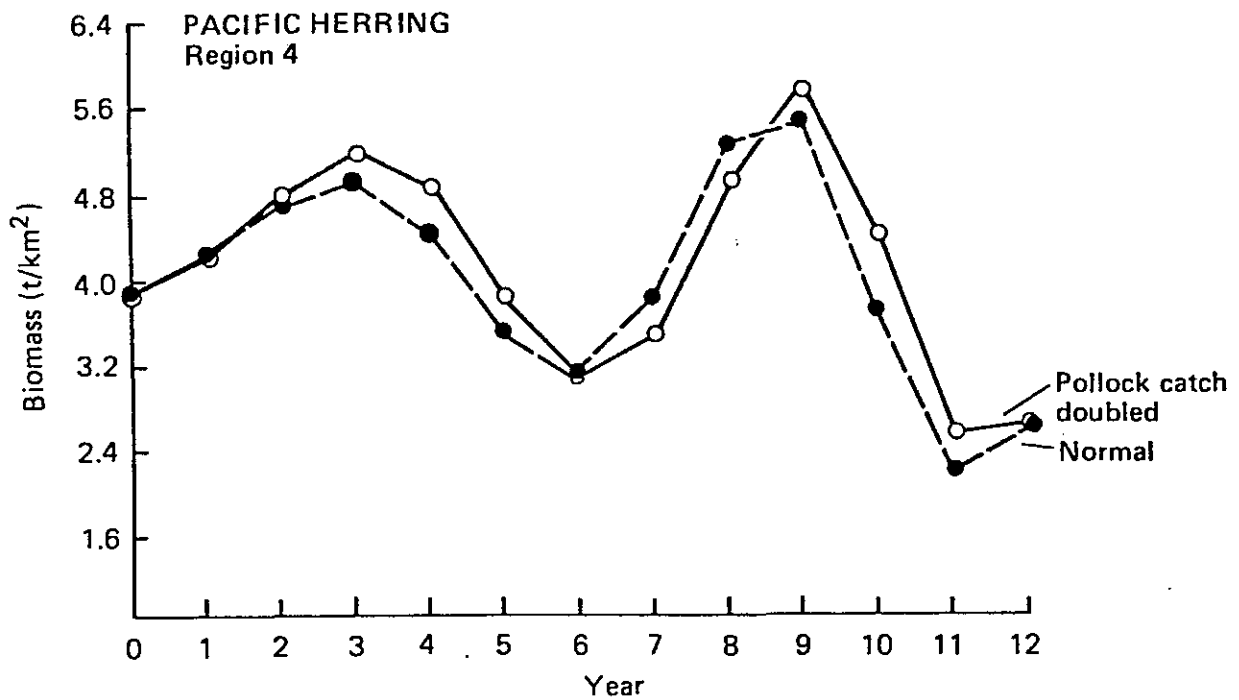
Figure 18.--Fluctuations of herring biomass in Region 4 in the Aleutian Region (see Figure 4) in "normal" condition and with pollock fishery doubled in this region.

Table 10.--Some typical annual rates of changes of biomasses (with reference to equilibrium biomasses) and typical periods and magnitudes of fluctuations of biomasses. $(\dfrac{B_1 - B_2}{B_e})$

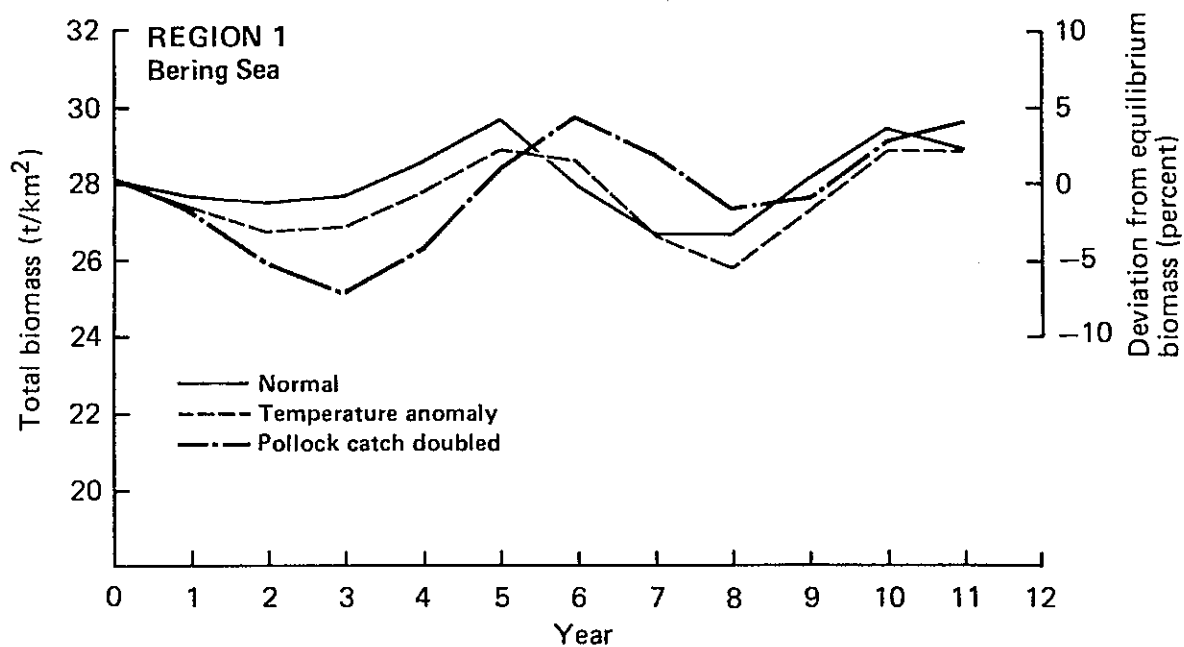| Species/ecological group	Annual change in percent of equilibrium biomass		Fluctuations	
	Range	Mean	Mean period, years	Mean magnitude (+%)
Flatfishes	7.5 to 13	10.5	6 to 7	45
Sculpins and other noncommercial demersal	8 to 26	12	5	40
Cod	7 to 20	13	7	35
Walleye pollock	11 to 34	19	5	75
Pacific herring	20 to 50	38	5	80
Squids	35 to 70	50	4	100
Benthos	65 to 80	75	4	120

Figure 19.--Fluctuations of total fish biomass in Region 1 in the Bering Sea
(see Figure 4) - in "normal" conditions" -- with temperature anomaly in
years 1 to 3 (-1.5, -2.5, -1.5°C, respectively); and -.- with present
pollock fishery doubled.

CONCLUSIONS AND FUTURE TASKS

The existing survey methods for evaluation of marine living resources are expensive and inaccurate. The conventional numerical models based on basic organic production and trophic levels are too simplistic and lacking in basic data to be useful for the evaluation of fish resources.

The large, holistic marine ecosystem simulations, which include all pertinent information, are coming into use for the evaluation of fishery resources and for the study of their dynamics. Using these models, equilibrium biomasses have been determined in a number of ocean regions in the northeast Pacific and estimates of the biomasses in other regions have been made on the basis of analogy.

The total finfish biomass varies from about 3 t/km^2 in low-latitudes open ocean to maximum 60 t/km^2 on high-productive continental shelves in medium latitudes. The North Sea finfish biomass is about 25 t/km^2 and the Bering Sea has about 37 t/km^2, of which about 12 and 16 t/km^2, respectively, is exploitable. Annual yield in both cases is about 7.5 t/km^2.

Individual biomasses fluctuate considerably from year to year. The average period of these fluctuations is 4 to 7 years (species dependent), and the magnitudes are about 35% to 80% of individual equilibrium biomasses. However, the highest biomass can be several times the lowest biomass. Rates of annual changes vary from about 8% of annual biomass (flatfishes) to about 45% (short-lived pelagic fish). Long-period fluctuations (decade to several decades) are superimposed to these shorter fluctuations.

The fluctuations are caused both by external factors, such as temperature anomalies, and by ecosystem internal factors, such as predation, cannibalism, and "year class rhythm" (i.e., the effects of the size of spawning biomass).

The total finfish population fluctuates but little from one year to another. Pronounced temperature anomalies have, however, some effect on the total biomass.

The effects of temperature anomalies on the biomasses of individual species vary from region to region and depend on acclimatization temperature and nature of the anomaly (e.g., + or -). Furthermore, forage species might be affected by the anomalies in opposite direction via changes in predator biomasses.

The fluctuations are also affected by fishery. Intensive fishery on one target species might cause an increase in forage species by decreased predation.

The manifold utility of the ecosystem and multispecies models has recently been fully demonstrated. In order to complete the evaluation of fishery resources, it is necessary to apply the ecosystem simulations for all ocean regions.

The ecosystem simulations require, as input, routinely observed fisheries data. These data collections should continue. We need to especially intensify the collection of trophodynamic data (i.e., stomach analyses for evaluation of space and time variable feeding). Furthermore, we need to improve fisheries survey techniques and intensify these surveys. Empirical studies on the turnover rates (annual production) of most marine ecological groups are also badly needed (e.g., benthos, squids, etc.).

Studies on migrations of most species are also lacking, including the studies of dispersal and aggregations in connection with trophodynamics (as density dependent regulation of predation).

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APPENDIX

Principal Formulas Used in Biomass Based Holistic Ecosystem Simulation

The biomass based ecosystem models PROBUB and DYNUMES have been described by Laevastu and Larkins (1981). Only the principal formulas are given in this appendix. A general scheme of computations, using monthly time step, is given in Figure 20.

Governing equations of ecosystem simulation

Biomass balance equation:

$$B_{i,t} = (B_{i,t-1}(1-e^{-g_{i,t}}) + B_{i,t-1}) \, e^{-(s+n)} - C_{i,t-1}$$

or

$$B_{i,t} = B_{i,t-1} \, e^{g_{i,t} - z_{i,t}}$$

where: $z_{i,t} = \phi_{i,t} + s_{i,t} + n_{i,t} + C_{i,t-1}$

$$C_{i,t-1} = \ell n \left(1 - (C_{i,t-1} / B_{i,t-1}) \right)$$

Yield equation:

$$Y_{i,t} = B_{i,t} \, e^{-\phi_{i,t}}$$

Trophodynamic equations:

The food requirement with unlimited food

$$R_{i,t} = B_{i,t} \, r_{i,t} \, \tau$$

Amount of species j in the food of species i

$$C_{j,i,t} = R_{i,t} \, \pi_{i,j}$$

Total consumption of species i

$$C_{i,t} = \sum_j C_{j,i,t}$$

BIOMASS
(First guess or previous time step)

+GROWTH ⟵ Empirical growth coefficient, adjusted
to temperature and recruitment changes

— SPAWNING STRESS MORTALITY

— FISHING MORTALITY

—PREDATION MORTALITY
(First guess or previous time step)

± MIGRATIONS
(DYNUMES only)

BIOMASS
(Time step 2)

FOOD CONSUMPTION

Food requirements

Food composition
(as modified by availability)

—PREDATION MORTALITY
(For next time step)

Repeat the computations for all species

Sum predation of all species
(At the end of time step)

Various monthly outputs

Repeat all in next time step
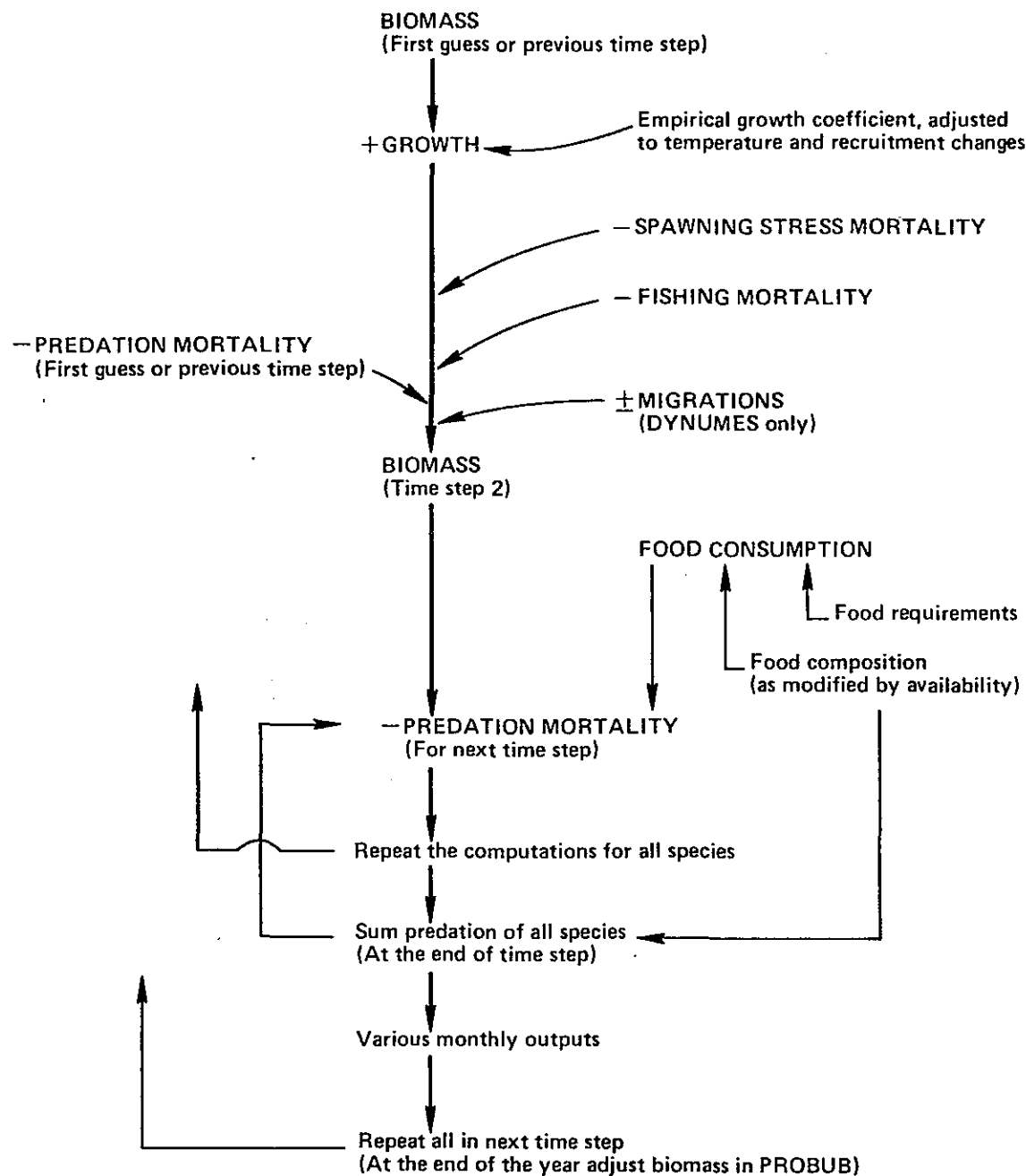(At the end of the year adjust biomass in PROBUB)

Figure 20.--Schematic flow diagram for most essential computations in PROBUB
and DYNUMES simulations.

Some transitive equations:

Seasonally changing growth rate

$$g_{i,t} = g_i^o + a_{g,i} \ (\cos\alpha t - \kappa_{i,g})$$

Effect of starvation on growth rate

$$g_{i,s} = g_i^o \ ((R_{i,t-1} - S_{i,t-1}) \ / \ R_{i,t-1})$$

where

R - ration in unlimited conditions

S - the "missing" part of R

Effect of temperature on growth rate

$$g_{i,t} = g_{i,s} \ e^{(\frac{1}{T_o} - \frac{1}{T})}$$

Density dependent yield

$$\phi_{i,t} = \phi_i^o \ (\bar{B}_i / B_{i,t})$$

Seasonally changing food requirement

$$r_{i,t} = r_i^o + d_{r,i} \ (\cos\alpha t - \kappa_{i,r})$$

Food requirement for growth and for maintenance

$$r_{i,t} = B_{i,t} \ (1-e^{-g_{i,t}})) \ k_g + B_{i,t} k_m \tau$$

Migrations

"Directed" migration

U pos.

$$UT_{(n,m)} = (B_{(n,m)} - B_{(n,m-1)}) \ / \ \ell$$

U neg.

$$UT_{(n,m)} = (B_{(n,m)} - B_{(n,m+1)}) \ / \ \ell$$

$$B_{(t,n,m)} = B_{(t-1,n,m)} - (T_d|U_{(t,n,m)}|UT_{(n,m)}) - (td|V_{(t,n,m)}|VT_{(n,m)})$$

Random migration

$$B_{(n,m)} = \alpha B_{(n,m)} + \beta(B_{(n-1,m)} + B_{(n+1,m)} + B_{(n,m-1)} + B_{(n,m+1)})$$

Equilibrium Biomasses
(and unique solution)

Definition: Equilibrium biomass is obtained if
biomass growth equals its removal by
predation and other mortalities, i.e.,
if all the biomasses in the ecosystem
in January in a given year are the same
as biomasses in January, previous year.

$$B_{i,t} = B_{i,t-1} \; e^{g_{i,t} - z_{i,t}}$$

Equilibrium if $g_{i,t} = z_{i,t}$ in all species

Where

g – determined from empirical data

z – computed in the model with many empirical inputs; part of predation

mortality is predetermined

Iteration by:

$$B_{i,t,12,0} = B_{i,t,12,a} + \frac{B_{i,b} - B_{i,a}}{k}$$

List of Symbols

$a_{g,i}$ — half magnitude of seasonally changing growth coefficient

$\bar{B}$ — equilibrium biomass

$B_{i,t}$ — biomass of species i, in time step t

$C_{i,t-1}$ — consumption of species i in time t-1

$d_{r,i}$ — half magnitude of seasonally changing food requirement

e — base of natural logarithms

$g_{i,t}$ — growth coefficient of species i at time t

k — iteration constant

k_g — food requirement for growth (ratio)

k_m — food requirement for metabolism parameter

ℓ — length of the grid

m — grid coordinate

n — mortality of old age; also grid coordinate

r_i — fraction of body weight required daily for maintenance

R_i — ration (normal food requirement)

s — spawning stress mortality

S — starvation in terms of fraction of missing food

t — time, [(t)-time step t; (t-1) - previous time step]

t_d — time in days (also length of time step)

T — temperature

T_o — optimum (acclimatization) temperature

U — u component of migration speed

UT — "upmigration" gradient of biomass (u direction)

V — v component of migration speed

VT — "upmigration" gradient of biomass (v direction)

z - total mortality (also total mortality coefficient)

α - phase speed

β - smoothing coefficient $= (1-\gamma/4)$

α_1, α_2 = phase speeds

ϕ_i - fishing mortality coefficient

$\kappa_{i,g}$ - phase lag of annual growth coefficient change

$\kappa_{i,r}$ - phase lag of food requirement

$\pi_{i,j}$ - fraction of species j in food of species i

τ - time step